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STUDIES ON THE TREMATODE FAMILY STRIGEIDAE (HOLOSTOMIDAE) NO. XIV. TWO NEW SPECIES OF DIPLOSTOMULA[1]

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THE purpose of this article is to present descriptions of two new species of strigeid metacercariae, together with a discussion of the characteristics and the nomenclature of the larval group (Diplostomulum) to which they belong and a comparative synopsis of the other known species.

Diplostomulum browni, sp. nov.[2]

During the summer of 1927 a single specimen of *Lymnaea emarginata angulata* Sowerby, heavily infected with a new

[1] Contribution from the Biological Station and from the Department of Zoology, University of Michigan. This is the fourteenth of a series of studies on the family Strigeidae by Professor George R. La Rue, his students and associates.

[2] Specimens referred to in this paper have the following numbers in the parasite collection of the Museum of Zoology of the University of Michigan: *Diplostomulum browni:* type slide, specimens mounted *in toto,* No. 261; paratypes mounted in sections, No. 262; paratypes in alcohol, No.

species of Diplostomulum larva, *Diplostomulum browni,* was found and presented to me by Dr. Harold W. Brown. This snail, taken from the northwestern part of Douglas Lake, Cheboygan County, Michigan, contained several hundred specimens of the present parasite together with a number of sporocysts producing an undetermined species of strigeid cercaria. The diplostomula were not encysted and occurred scattered throughout the soft parts of the host; indeed, many were found within the sporocysts mentioned above. These were also not encysted. During the summer a great many snails of several species were carefully examined for parasites by a number of investigators at the Biological Station, but no others were found to be infected with diplostomula. So far as I am aware this is the first record of the occurrence of a diplostomulum parasitic in snails.

Careful studies were made of both living and preserved material. The study of living specimens was especially useful in working out the details of the excretory system, the vessels of which are so small and delicate that it is almost impossible to trace them in preserved animals. The minutiae of the excretory pattern are most clearly visible in living worms mounted in water and under considerable pressure of a coverglass. It is regrettable that an opportunity for making a large series of measurements of living specimens was not afforded. For whole mounts and sections, specimens were fixed in sublimate-acetic and stained *in toto* in Ehrlich's acid haematoxylin made very dilute with 70 per cent alcohol. The sections were decolorized on the slide and counterstained with eosin.

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210. *D. corti:* type specimen mounted *in toto,* No. 288; paratypes mounted *in toto,* Nos. 289–294; paratypes mounted in sections, Nos. 295–300. *D. spathaceum:* specimens mounted *in toto,* No. 276; specimens mounted in sections, No. 277. *D. petromyzi-fluviatilis:* specimens mounted *in toto,* No. 269; specimens mounted in sections, No. 270. *D. phoxini:* specimens mounted *in toto,* No. 275. *Tetracotyle sp.* identified by Dr. F. Zandt as *Diplostomum cobitidis:* specimens mounted *in toto,* No. 250.

For purposes of comparison specimens of *Diplostomulum spathaceum* (Rudolphi) (synonym, *Diplostomum volvens* von Nordmann), *Diplostomulum phoxini* (Faust), presented to Professor La Rue by Professor L. Scheuring of München, and *Diplostomulum petromyzi-fluviatilis* (Diesing), presented by Professor E. S. Goodrich of Oxford, were stained and mounted as outlined above.

The body of the parasite comprises two well-defined regions, the fore- and hind-bodies. In living specimens the fore-body is thin, foliaceous, ovate in outline, longitudinally elongate, slightly concave ventrally and slightly convex dorsally. In preserved specimens the concavity of the ventral surface is lost. The relatively small hind-body is present as a hemispherical appendage on the dorsal side of the posterior end of the fore-body. The oral sucker (Fig. 5*os*) is antero-terminal, with the mouth opening directed ventrad. The so-called lateral suckers (Fig. 5*ls*) are usually extended as short papillae, but may be withdrawn to form shallow cup-shaped depressions. In preserved specimens the lateral suckers usually appear as slight inconspicuous projections of the antero-lateral margins of the body. The ventral sucker (Fig. 5*ac*), located at the anterior end of the posterior half of the fore-body, is slightly smaller than the oral sucker. The hold-fast organ (Fig. 5*hf*), situated immediately behind the acetabulum, is somewhat larger than the acetabulum. The cuticula of the entire body is uniformly armed with minute quincuncially arranged spines. Four living worms, under cover-glass pressure, varied in length from 0.247 mm. to 0.277 mm. (average 0.262 mm.), and in width from 0.182 mm. to 0.211 mm. (average 0.189 mm.). The principal measurements of ten specimens mounted *in toto* are given in Table I.

The parasites were very active when removed from the tissues of the snail and placed in water. The movements consisted of alternately lengthening and shortening the body by means of which processes no spatial locomotion was accomplished. Occasionally, however, a specimen was observed crawling on the bottom of the container, after the manner of

TABLE I

Measurements in Millimeters of Ten Mounted Specimens of Diplostomulum browni

	Minimum	Maximum	Average
Body			
length	0.162	0.233	0.206
width	0.106	0.141	0.127
Oral sucker			
diameter	0.028	0.035	0.033
Pharynx			
length	0.021	0.028	0.022
length	0.024	0.032	0.027
Acetabulum			
width	0.028	0.035	0.032
length	0.042	0.053	0.046
Hold-fast organ			
width	0.035	0.053	0.047

a leech, or on the under side of the surface film of the water, using the oral sucker and acetabulum for attachment.

The digestive tract comprises the usual parts. The pharynx (Fig. 5*ph*) is large and muscular, the prepharynx and oesophagus (*oe*) short. The caecal furcae (Figs. 5, 8*int*) extend well into the hind-body. In living specimens the caeca often contain irregularly shaped granules of solid substance which surge back and forth in response to movements of the body. Of the nervous system only the suprapharyngeal commissure (Fig. 5*sp*) and the anterior (*an*) and posterior (Figs. 5, 8*pn*) pairs of nerve trunks were observed. The posterior trunks were traced back to the regions postero-lateral to the hold-fast organ. The reproductive system is represented by a single heavily staining mass of cells (Fig. 5*rf*) situated in the proximal part of the hind-body in the septum between the halves of the urinary bladder. The body is provided with subcuticular transverse (Fig. 8*cmf*) and longitudinal (*lmf*) muscle fibers. Other muscle fibers were not observed. Scat-

tered throughout the parenchyma are large unicellular glands the ducts of which communicate directly with the surface. In living specimens the mouths of the ducts of these glands are plugged by papilliform accretions of the exudate. A distinct compact adhesive gland associated with the hold-fast organ was not observed.

The excretory system closely resembles that of *Diplostomulum spathaceum* (Rudolphi) which was studied by Claparède (1858) and more carefully by Fraipont (1880) and Zandt (1924). The primary excretory apparatus, consisting of flame cells and associated tubules, is greatly obscured by the thickness of the animal and the extensive development of the reserve bladder. Many flame cells and scattered tubules were observed, but not in sufficient detail to give any definite idea of their arrangement. The bilobate urinary bladder (Fig. 7*ub*) occupies the greater part of the hind-body. Its two halves, separated anteriorly by a median septum, are joined posteriorly and communicate with the dorso-terminal excretory pore (*ep*) through a short duct (*ed*). The halves of the urinary bladder, inflated in the hind-body, extend into the fore-body as narrow tubules, to the region antero-lateral to the acetabulum. At the level of the hold-fast organ (*j*) the tubular portions of the urinary bladder receive the common trunks of the *primary excretory apparatus*. The common trunks are short and each bifurcates, giving rise to an *anterior* and a *posterior primary collecting tubule* (*apt, ppt*). These were traced to the anterior and posterior reaches of the body, respectively, but their exact relationship to the flame cells was not determined. The principal tubules of the primary excretory apparatus lie dorsal to those of the reserve bladder. The fact that the flame cells in *Diplostomulum spathaceum* are associated with a pair of longitudinal tubules, not related directly to the vesicles containing calcareous corpuscles, was observed by Fraipont (1880: 432) and Zandt (1924: 237). The relationship, however, of these tubules to the urinary bladder was not clearly understood. Fraipont considered that each longitudinal tubule associated with flame

cells communicates with the rest of the excretory system at two and probably three different points, whereas Zandt considered that they empty directly into the posterior portions of the urinary bladder.

In the regions antero-lateral to the acetabulum the tubular portions of the urinary bladder give rise to two pairs of vessels which connect with the tubules of the reserve bladder. These are the *lateral collecting vessels* (Fig. 7*lc*) and the *posterior transverse commissural vessels* (*pc*). The *posterior transverse commissural vessels* extend mesad to join the *median dorsal vessel* (*md*). The lateral collecting vessels extend antero-laterad and soon bifurcate, giving origin to the *antero-lateral* (*al*) and *postero-lateral vessels* (*pl*). The antero-lateral vessels extend forward to the regions near the oral sucker where they are joined to the anterior end of the median dorsal vessel by the *anterior transverse commissural vessels* (*ac*). The postero-lateral vessels extend posteriad, lateral to the tubular portions of the urinary bladder, and end blindly near the median line in the posterior part of the fore-body. The median dorsal vessel (*md*), formed by the union of the anterior transverse commissural vessels, extends posteriorly, ending blindly dorsal to the hold-fast organ. The median dorsal, anterior transverse commissural, antero-lateral and postero-lateral vessels receive many short branches, often dendritic, the distal termini of which are inflated as small spherical vesicles each containing a spherical calcareous concretion (*cc*). The vesicles and the calcareous corpuscles contained in them are somewhat uniform in size and are arranged in two layers, near the ventral and dorsal body-walls. The number of such vesicles and the size of the corpuscles vary greatly in different individuals.

Diplostomulum corti, sp. nov.

This description is based upon notes and sketches and a number of preserved specimens, some sectioned and some mounted *in toto,* kindly given to me by Professor W. W. Cort, who made a preliminary study of this form but neglected to

publish his discoveries. The parasites upon which the observations were made were found encysted in the muscles and particularly at the bases of the fins of *Ameiurus melas* (Rafinesque) and *Ameiurus nebulosus* (Le Sueur) obtained from the Illinois River during November and December, 1909. Five of fifteen fish examined were found to be infected, one so heavily that the muscles were almost entirely filled with the trematodes. The cyst was composed of a loose sac of connective tissue, probably entirely of host origin. When removed from the cysts the larvae moved actively, but the nature of the movement was not recorded.

In form *Diplostomulum corti* (Fig. 6) resembles *Diplostomulum browni,* but is considerably larger. The ventral surface of the fore-body is more concave, the posterior end is curved ventrad forming a transverse fold. The hind-body is much larger. The acetabulum (*ac*) and greater part of the hold-fast organ (*hf*) lie anterior to the middle of the body and the lateral suckers (*ls*) are much more deeply cupped.

TABLE II

Measurements in Millimeters of Preserved Specimens of Diplostomulum corti

Number of Specimen	1	2	3	4	Average
Body					
length	0.81	0.70	0.85	0.88	0.81
width	0.50	0.40	0.47	0.53	0.475
Distance of acetabulum from anterior end	0.28	0.25	0.29	0.26	0.27
Oral sucker, diameter	0.066	0.062	0.066	0.072	0.067
Pharynx					
length	0.053	.....	0.045	0.040	0.045
width	0.036	.....	0.026	0.038	0.033
Acetabulum, diameter	0.073	0.073	0.073	0.083	0.076
Intestinal caecum, length	0.098	.....	0.079	0.075	0.081
Oesophagus, length	0.015	.....	0.019	0.021	0.019

The pharynx (*ph*) is relatively smaller, the digestive caeca (*int*) are larger in diameter, and the reproductive fundament (*rf*) is more differentiated. No attempt was made, however, to interpret the various elements of the reproductive complex. A bursa copulatrix is present (not shown in figure). A large, distinct, longitudinally trilobate hold-fast gland (*hfg*) occurs. In the position of the acetabulum and hold-fast organ anterior to the middle of the body, the extensive development of the hold-fast gland and the presence of a bursa copulatrix, *Diplostomulum corti* differs from all other described species of diplostomula. The nervous and excretory systems were not studied. The principal measurements of four mounted specimens are shown in Table II.

Discussion

The oldest known species of the larval group Diplostomulum is *Diplostomulum spathaceum* (Rudolphi), which was described by von Nordmann (1832: 28) as *Diplostomum volvens*. Braun (1894a: 680) showed that according to a feeding experiment performed by the Ehrhardt brothers *Diplostomum volvens* von Nordmann is the larva of *Hemistomum spathaceum* (Rudolphi 1810) Diesing 1850. The name Hemistomum Diesing (1850: 287) falls as a synonym of Alaria Schrank (1788: 52) of which *Alaria alata* (Goeze) is the type species. La Rue (1926a: 15), regarding *Hemistomum spathaceum* (Rudolphi) Diesing as non-congeneric with *Alaria alata*, proposed to make it the type species of a new genus Proalaria. Since, however, *Diplostomum volvens* is the larva of *Hemistomum spathaceum*, it follows that the name of this genus should be Diplostomum von Nordmann [type species, *Diplostomum spathaceum* (Rudolphi)] and the name Proalaria La Rue therefore becomes a synonym. The respective species recognized under the name Proalaria by La Rue (1926b: 277) severally become *Diplostomum spathaceum* (Rudolphi) Olsson, *Diplostomum gavium* (Guberlet) mihi, *Diplostomum indistinctum* (Guberlet) mihi, *Diplostomum confusum*

(Krause) mihi, *Diplostomum excavatum* (Rudolphi) mihi, (?) *Diplostomum intermedium* (Johnston) mihi, (?) *Diplostomum triangulare* (Johnston) mihi and *Diplostomum trilobum* (Rudolphi) mihi. Also *Proalaria huronensis* La Rue (1927: 26) becomes *Diplostomum huronense* (La Rue) mihi. The name Diplostomum, proposed by Brandes (1888: 50) as a new genus (not of von Nordmann, 1832) for certain species of Strigeidae, falls as a homonym.

Now that Diplostomum von Nordmann is a generic name in good standing, it can no longer be used to designate a larval group and it therefore becomes necessary to find another name for that purpose. Brandes (1892: 511), discussing the taxonomy of *Monostomum constrictum* Diesing (1850), made the following statement: "*Monostomum constrictum* Dies., aus dem Auge von Abramis brama, halte ich für eine Form, die zur Unterfamilie der Diplostomen gehört; demnach würde ich die Art als Diplostomulum constrictum bezeichnen." Stiles and Hassal (1908: 156) interpreted this statement to mean that the name Diplostomulum was being proposed as a collective group name and it has since been used in that sense by Faust (1917: 66) and Ward (1918: 411). It is very doubtful that *Monostomum constrictum* is a strigeid larva. It seems desirable, however, to retain Diplostomulum as a group name and to use it for those metacercariae closely resembling *Diplostomum volvens*. Inasmuch as *spathaceum* Rudolphi (1819: 403) has priority over *volvens* von Nordmann (1832: 28), the larva *Diplostomum volvens* von Nordmann becomes *Diplostomulum spathaceum* (Rudolphi) mihi.

It has been the custom of many authors to regard as belonging to a separate larval group (Tylodelphys Diesing, 1850) certain elongate species most of which have all the characters diagnostic of the larval group Diplostomulum (as outlined below), but in which the lateral suckers and the hind-body are not well developed or clearly defined. These differences, in my opinion, are not sufficient to separate these larval groups. The pattern of the reserve bladder of *Tylodelphys clavata* (von Nordmann), the type species, according to von Nord-

mann (1832: Taf. II, fig. 5) and Claparède (1858: Taf. VIII, figs. 2, 3), is not materially different from that of *Diplostomulum browni* and *D. spathaceum*. As a name for the combined group, preference is given to Diplostomulum over Tylodelphys for the reason that the latter may, when the life-history of *Tylodelphys clavata* is known, attain good standing as the generic name of an adult form, since Tylodelphys was not proposed as a larval group name. The species which have been assigned to Tylodelphys are in general more elongate than other diplostomula, since the width of the body is usually less than half the length. They differ also from most diplostomula in that they have ellipsoidal rather than spheroidal calcareous concretions.

The larval group, Diplostomulum, may be redefined as embracing strigeid metacercariae having the following characteristics: (1) fore-body foliaceous, concave ventrally; (2) hind-body present as a small conical prominence on the postero-dorsal part of the fore-body; (3) *reserve bladder* comprised of a system of more or less definitely arranged tubules with calcareous corpuscles, round or ellipsoidal, disposed in vesicles at the termini of small branches; (4) usually a pair of lateral organs (the so-called lateral suckers) on the antero-lateral edges beside the oral sucker; and (5) no true cyst of parasite origin.

Comparative Synopsis of Other Described Diplostomula

1. *Diplostomulum spathaceum* (Rudolphi) mihi

Diplostomum volvens	von Nordmann (1832: 28)
Diplostoma volvens, Nordmann	Cobbold (1860: 50)
Tetracotyle volvens	Mataré (1910: 27)
Diplostomulum volvens	Faust (1917: 66)

Descriptions of *Diplostomulum spathaceum*, based primarily upon the original by von Nordmann (1832: 28), have been published by Creplin (1839: 289), von Nordmann (1843), Diesing (1850: 306, and 1858: 317), Zschokke (1884: 207), Hofer (1904: 294), Lühe (1909: 165), Zandt (1924: 236)

and Plehn (1924: 147). In these descriptions and the reports of Rayer (1843), Dujardin (1845: 474), Creplin (1846: 150, 153), Krøyer (1852–53: 1224), Braun (1892: 796), Olsson (1893: 9) and Fehlmann (1916), *Diplostomulum spathaceum* has been listed from various parts of Europe and from the following fishes: *Scardinius erythrophthalmus, Chondrostoma nasus, Perca fluviatilis, Lucioperca lucioperca, Lucioperca sandra, Acerina cernua, Lota lota, Lota communis, Leuciscus rutilus, Leuciscus vulgaris, Leuciscus phoxinus, Abramis brama, Squalius cephalus, Esox lucius.* The parasites have been found in various parts of the eyes of the hosts infected. For North America Cooper (1915: 191) reported the finding of parasites, which he identified as *Diplostomum volvens,* in the eyes of *Micropterus dolomieu* Lacépède. Steenstrup (1845: 97) suggested that the four forms described by von Nordmann from the eyes of fishes, viz. *Diplostomum clavatum, Holostomum cuticola, Holostomum brevicaudatum* and *Diplostomum volvens,* represent successive stages in the life-cycle of a single species. Claparède (1858: 100; Taf. VIII, figs. 4–5) worked out the relationship of the calcareous corpuscles to the vessels of the reserve bladder. Fraipont (1880: 432) discovered that the flame cells are not associated directly with the vessels of the reserve bladder, a question previously discussed in connection with the excretory system of *Diplostomulum browni.* Braun (1894a, b, and c) reported on feeding experiments performed by the Ehrhardt brothers which demonstrated that *Diplostomulum spathaceum* becomes *Diplostomum spathaceum* in the intestines of *Larus ridibundus* and *Sterna hirundo.* An attempt of the Ehrhardt brothers to cause miracidia of *Diplostomum spathaceum* to penetrate the eyes of goldfish and develop directly (metastatically) into metacercariae was unsuccessful. Roth (1904: 294), however, was of the opinion that such is the manner of the development. Szidat (1924) demonstrated that *Diplostomulum spathaceum* develops from a furcocercous cercaria, that it is therefore digenetic in development, and that the cercaria gains entrance into the host by active penetration through the skin of any

part of the body, seeking the eyes afterward, rather than by direct penetration through the cornea. He also obtained additional evidence in confirmation of the results of the Ehrhardt brothers in regard to the further development of the metacercaria. Salzer (1907) made a careful study of the cataract produced by *D. spathaceum* in the eyes of trout.

A figure by Fraipont (1880: Pl. XVIII, fig. 18) shows that the arrangement of the vessels of the reserve bladder in *Diplostomulum spathaceum* is practically the same as in *Diplostomulum browni*; however, the presence in the former of vesicles containing calcareous corpuscles associated directly with the tubular portions of the urinary bladder constitutes a notable difference. All of several specimens of *Diplostomulum spathaceum* taken from *Cobitis barbatula,* collected near Breslau, Germany, and sent to Professor La Rue by Professor L. Scheuring, are a little larger and relatively much broader than *Diplostomulum browni.* The lateral suckers in these specimens are represented by broad, shallow depressions (Fig. 1), whereas in *D. browni* the lateral organs project slightly (Fig. 5*ls*). These differences in the general shape of the body and the form of the lateral suckers, although constant in the material which I have examined, may be due to the different method of fixation, since the specimens of *D. spathaceum* were fixed in the host tissues in Bouin's mixture, whereas those of *D. browni* were separated from the host tissues and fixed in sublimate-acetic. Although the two forms are morphologically much alike, it seems probable that the occurrence of *D. browni* in a snail host is a physiological character of specific importance, since *D. spathaceum* has never been reported from snails in Europe.

2. *Diplostomulum lenticola* (von Linstow) mihi

Diplostomum lenticola	von Linstow (1878b: 226)
Tetracotyle lenticola von Linstow	Braun (1892: 796)
Tetracotyle lenticola	Mataré (1910: 497)
Tetracotyle lenticola (von Linstow)	Faust (1918: 77)

Descriptions of *Diplostomulum lenticola* based upon the original description of von Linstow (1878b: 226, Taf. VII,

fig. 9) have been published by Lühe (1909: 766) and Faust (1918: 77). This form, which has been listed only from the eyes of *Abramis vimba,* closely resembles *Diplostomulum spathaceum,* differing from it chiefly in that the acetabulum relative to the size of the oral sucker is proportionately smaller. Zandt (1924: 237), however, finds that in the diplostomula from the eyes of various fishes examined by him, the relative sizes of the oral sucker and acetabulum vary greatly in different individuals and considers that they all probably belong to the same species. Whether *Diplostomulum lenticola* is a distinct species is, therefore, a matter that requires further investigation.

3. *Diplostomulum petromyzi-fluviatilis* (Diesing) mihi

Entozoa from *Petromyzon fluviatilis*	Müller (1840: 198)
Diplostomum rachineum	Müller (1842: 20)
Diplostomum petromyzi fluviatilis Müller	Diesing (1850: 307)
(?) *Diplostomum* sp. *in Petromyzon fluviatilis*	Krøyer (1852–53: 1051)
Tylodelphys (?) *Petromyzonis fluviatilis*	Diesing (1858: 316)
Diplostoma, Mülleri, Cobbold	Cobbold (1860: 50)
Entozoa in *Petromyzon planeri*	Gulliver (1870: 849)
Neuronaia lampetrae	Gulliver (1872: 103)
Tylodelphys (?) *Petromyci fluviatilis* Diesing	von Linstow (1878a: 290)
Neuronaina Lampretae Gulliver	von Linstow (1878a: 290)
Tetracotyle Petromyzontis	Brown (1899: 489)
Tylodelphys petromyzi fluviatilis Diesing	Lühe (1909: 168)
Tetracotyle petromyzi	Mataré (1910: 496)

This species, found and reported by Müller (1840: 198) and briefly described by Gulliver (1870: 849; fig. 9), was carefully studied by Brown (1899), from whose description others have been published by Lühe (1909: 168) and Faust (1918: 77). It has been reported from the cranial and brain cavities of both *Petromyzon fluviatilis* and *P. planeri* in Europe. According to Brown (1899, Pl. 39, fig. 5), many

gland cells are associated with the lateral suckers, a feature which has not been reported for other species of Diplostomulum. In preserved specimens sent to Professor La Rue by Professor E. S. Goodrich, of Oxford, the lateral suckers are more deeply cup-shaped (Fig. 2) than in any other described species of diplostomula; and when everted they become, accordingly, more prominent (Fig. 4). In *D. browni* (Fig. 8) and *D. spathaceum* the concavity of the ventral surface is lost and the fore-body is somewhat thickened in the process of fixation. Sections of *D. petromyzi-fluviatilis* show the ventral surface to be distinctly concave and the fore-body relatively thin.

Inasmuch as a satisfactory series of measurements of *Diplostomulum petromyzi-fluviatilis* has never been recorded, those which I have made of ten specimens mounted *in toto* are presented in Table III.

TABLE III

Measurements in Millimeters of Ten Mounted Specimens of Diplostomulum petromyzi-fluviatilis

	Minimum	Maximum	Average
Body			
length	0.225	0.289	0.257
width	0.211	0.261	0.239
Oral sucker			
length	0.042	0.053	0.050
width	0.042	0.053	0.046
Pharynx			
length	0.031	0.049	0.041
width	0.017	0.025	0.021
Acetabulum			
length	0.031	0.049	0.038
width	0.053	0.060	0.056
Hold-fast organ			
length	0.063	0.109	0.076
width	0.105	0.112	0.106
Cavity of lateral sucker,			
depth	0.024	0.035	0.030

4. *Diplostomulum phoxini* (Faust) mihi

Tetracotyle from brain of *Phoxinus laevis*	Mataré (1910)
Tetracotyle phoxini	Faust (1918: 77)
Tylodelphys from *Phoxinus laevis*	André (1918: 13)
Tetracotyle phoxini Mataré	Mathias (1925: 17)
Tetrocotyle phoxini (Faust)	Ashworth and Bannerman (1927: 167)

This species was described in detail by Mataré (1910) and briefly by André (1918), the descriptions being based upon specimens from the brain and cranial cavity of *Phoxinus laevis,* from different parts of Switzerland. The name *Tetracotyle phoxini* was applied to Mataré's description by Faust (1918: 77). Mataré's specimens, measured apparently in life, averaged 0.2 mm. in length and 0.15 mm. in width. Those of André, preserved and sectioned, were, on the average, 0.23 mm. long and 0.15 mm. wide. Ashworth and Bannerman (1927) described in detail a Diplostomulum found in the brain and cranial cavity of *Phoxinus phoxinus* from near Edinburgh. Although their discoveries in regard to minutiae of the excretory and nervous systems differ somewhat from the findings of Mataré and their specimens were a little larger (from 0.27 mm. to 0.42 mm. in length, in life), they were of the opinion that their material was identical with *Tetracotyle phoxini* Faust. Ten of several preserved diplostomula, taken from the brain and cranial cavity of *Phoxinus laevis* from Lunz and presented to Professor La Rue by Professor L. Scheuring, of München, varied in length from 0.203 mm. to 0.276 mm. (average 0.219 mm.) and in width from 0.109 mm. to 0.131 mm. (average 0.121 mm.). These specimens are probably identical with Mataré's species, and their measurements, allowing for shrinkage in the process of fixation, correspond favorably with those of Ashworth and Bannerman. According to both Mataré (1910: 510) and Ashworth and Bannerman (1927: 163), the cuticula is entirely without spines, an unusual circumstance for strigeid larvae. The calcareous concretions are more or less spherical (Ashworth and Bannerman, 1927: Figs. 5–6). In most of our specimens the lateral suckers have the form shown in Fig. 3.

5. *Diplostomulum heterobranchi* (Wedl) mihi

Monocerca heterobranchi Wedl (1861: 478)
Tetracotyle heterobranchi Mataré (1910: 497)

This parasite, found in thousands in adipose tissue about the brain of *Heterobranchus anguillaris* in Egypt, was described briefly by Wedl (1861: 478; Taf. III, fig. 39). According to the figure, the body of the parasite is elongate like that of a Tylodelphys; the calcareous concretions, however, are spheroidal. The presence of a hind-body was not indicated.

6. *Diplostomulum putorii* (von Linstow) mihi

Diplostomum putorii von Linstow (1877: 191)
Tetrocotyle putorii Mataré (1910: 497)

This worm, found encysted in the gut and oesophagus of *Foctorius putorius,* was briefly described by von Linstow (1877: 191; Taf. XIV, fig. 21). According to the figure, the animal is pointed anteriorly and without lateral suckers; the calcareous concretions are spheroidal and the pharynx is larger than the oral sucker. This is the only Diplostomulum recorded from a mammal. The presence of a hind-body was not indicated.

7. *Diplostomulum odhneri* (Travassos) mihi

Larva of a Prohemistomum Travassos (1924: 836)

This form was found encysted beneath the skin of *Haemulon sp.* in Brazil and briefly described by Travassos (1924: 836; fig. 1). According to the figure, the animal is without lateral organs and a hind-body. The acetabulum is somewhat smaller than the oral sucker. Nothing is said concerning the excretory system. No fundament of reproductive organs could be found. By a feeding experiment the larvae were developed into *Prohemistomum odhneri* Travassos in the intestines of *Nyctanassa violacea* L.

8. *Diplostomulum nanus* (Stiles and Goldberger) mihi

Agamodistomum nanus Stiles and Goldberger (1908: 30)

This species was described by Stiles and Goldberger (1908) from specimens taken from the pectoral muscles of *Francolinus*

subtorquatus from Benguella, West Africa. Through the courtesy of Dr. C. W. Stiles, of Washington, D. C., to Professor La Rue, I have had an opportunity to examine type and cotype material of *Agamodistomum nanus*. The structure referred to by Stiles and Goldberger (1908, fig. 45) as a "genital pore" is the external opening of the cavity of a hold-fast organ and the anterior "primordium of genital glands" (fig. 52) is the hold-fast gland. The species is in reality, therefore, a Diplostomulum.

9. *Diplostomulum vegrandis* (La Rue) mihi

Cercaria vegrandis La Rue (1917: 8)

This species was found encysted in the fat bodies of *Thamnophis marciana* (Baird and Girard) and *Thamnophis eques* (Reuss) from western Texas and described by La Rue (1917: 8; Pl. 1, figs. 2, 3, 4). The description is based upon preserved material and it was not possible to study the details of the excretory system and the shape of the calcareous concretions. The round or oval cavities found in the parenchyma probably represent vacuities in which lay calcareous corpuscles. Lateral suckers are not present and a hind-body was not observed. Through the courtesy of Professor La Rue I have been able to examine type and paratype material of this species. The structure described as "probably the genital pore" is clearly homologous to the hold-fast opening in strigeid larvae. The species is, therefore, a Diplostomulum.

10. *Diplostomulum sirtali* (Nicoll) mihi

Diplostomum sirtali Nicoll (1912: 767)

This parasite, encysted in the mesenteric fat of three-striped snakes, *Tropidonotus ordinatus sirtalis* [*Thamnophis sirtalis sirtalis* (Linné)], was found and described by Nicoll (1912: 769; fig. 107). These snakes, originally from North America, died in the Gardens of the Zoological Society of London. The conditions under which the snakes had been kept were not recorded and it is not possible to determine whether

they acquired their infections in England or America. Since, however, a similar parasite is not known to occur in European snakes, it seems probable that it is an American form. *D. sirtali* is somewhat similar to *D. vegrandis*, from which it differs in that it is rather larger and that the fore-body is distinctly concave ventrally, the hind-body is plainly visible and the acetabulum is slightly anterior to the middle of the body—differences which may be due, at least in part, to the fact that *D. sirtali* was described in life, whereas *D. vegrandis* was described from preserved material. Although the arrangement of excretory vessels was not studied, the presence of calcareous corpuscles distributed throughout the body was observed.

11. *Diplostomulum rhachiaeum* (Henle) mihi

Parasite from *Rana esculenta* and *R. temporaria*	Caldani (1794: 312)
Vermes generis dubii ranarum	Rudolphi (1810: 268)
Diplostomum rhachiaeum	Henle (1833: 19)
Diplostomum rachiaeum	Dujardin (1845: 475)
Tylodelphys rhachidis Diesing	Diesing (1850: 305)
Tylodelphis rhachidis	Pagenstecher (1857a: 38)
Diplostoma rhachiaeum, Henle	Cobbold (1860: 49)
Diplostomum rachieum	Fraipont (1880: 419)
Diplostomum (*Tylodelphis*) *rachidis*	Parona (1896: 2)
Tylodelphys rhachiaea (Henle)	Lühe (1909: 168)
Tetracotyle rhachiaea	Mataré (1910: 496)

This species, found encysted in the vertebral canal and in the viscera of *Rana esculenta* and *R. temporaria*, described and figured, but not named, by Caldani (1794: 312; Pl. 7, figs. 7, 8), is perhaps the oldest known strigeid metacercaria. Not aware of Caldani's report, Henle (1833) again described the species as new. Other descriptions based on that of Henle have been published by Dujardin (1845: 475), Diesing (1850: 305), Pagenstecher (1857: 38) and Lühe (1909: 168). The measurements recorded by Pagenstecher were original. The association of the ovoidal calcareous corpuscles with the excretory tubules was shown by Claparède (1858: 99; Taf. VIII, figs. 1, 2, 3). The body is elongate, its length being more than

twice its width. The lateral suckers are visible as ear-like processes only in certain contraction states (Henle, 1833, fig. 19). The hind-body is not clearly set off from the fore-body.

12. *Diplostomulum clavatum* (von Nordmann) mihi

Diplostomum clavatum	von Nordmann (1832: 42)
Tylodelphys clavata Diesing	Diesing (1850: 305)
Diplostoma clavatum, Nordmann	Cobbold (1860: 49)
Tetracotyle clavata	Mataré (1910: 496)

Descriptions of this species based on the original by von Nordmann (1832: 42) have been published by von Nordmann (1843), Dujardin (1845: 475), Diesing (1850: 305) and Lühe (1909: 168). In these descriptions and the reports of Krøyer (1846–53: 253) and Zandt (1924: 241), it has been listed from the eyes of the following hosts: *Perca fluviatilis, Lucioperca lucioperca, Acerina cernua, Esox lucius, Abramis brama, Barbus fluviatilis, Squalius cephalus, Leuciscus leuciscus, Leuciscus rutilus,* and *Salmo salvelinus.*

Diplostomulum clavatum closely resembles *D. rhachiaeum* in regard to the general shape of the body, the shape and the arrangement of the calcareous corpuscles, the structure of the lateral suckers and the condition of the hind-body.

13. *Diplostomulum craniarium* (Diesing) mihi

Trematodum from cranial cavity of *Cobitis fossilis*	Leydig (1853: 382)
Tylodelphys (?) *craniaria*	Diesing (1858: 316)
Diplostoma craniarium, Cobbold	Cobbold (1860: 49)
Tylodelphis craniaria Dies.	Braun (1892: 796)
Tylodelphys craniaria	Pavesi (1881: 616)
Tylodelphys craniaria	Mataré (1910: 496)

This species was found in the cranial cavity of *Cobitis fossilis,* described and figured, but not named, by Leydig (1853: 382; Taf. XIV, fig. 6). Leydig confused the anterior and posterior regions of the body, and the digestive and excretory systems. His figure, however, shows the body to be elongate and the calcareous corpuscles ovoidal. Brief descriptions based on that of Leydig were published by Diesing (1850:

316) and Lühe (1909: 168). The occurrence of the parasite has been reported only once.

14. *Diplostomulum joyeuxi* mihi

Metacercaria (*Diplostomum*) sp. Joyeux (1923: 334)

This parasite, described and figured by Joyeux (1923: 334; fig. 3), occurs encysted in the muscles of *Rana esculenta ridibunda* Pallas in Tunis, Africa. As represented in the figure, lateral suckers and hind-body are apparently wanting; the development of the reproductive system is well advanced, with testes, ovary, uterus, genital pore and vitellaria differentiated; the excretory system is very simple, consisting of "un collier entourant le pharynx, deux troncs longitudinaux decendant le long du corps et se réunissant à l'extrémité postérieure pour former un pore excréteur." The author does not state whether observations were made on living material. If only preserved material was studied, it is possible that the "collier entourant le pharynx" pertains to the nervous system and that the nervous and excretory systems were, in part, confused. This assumption is supported by the fact that in preserved specimens, mounted *in toto,* of *Diplostomulum browni, D. spathaceum,* and *D. petromyzi-fluviatilis,* the posterior ends of posterior nerve trunks are superimposed upon the tubular portions of the urinary bladder, whereas other parts of the excretory system are not recognizable. The presence of calcareous corpuscles was not mentioned.

Species Inquirendae

Inasmuch as it is doubtful that the following species belong to the larval group Diplostomulum, they are listed under their oldest known names.

1. *Diplostomum parvulum* Stafford

Tetracotyle parvula Mataré (1910: 497)
Diplostomulum parvulum Faust (1917: 66)

The type specimens of this species were taken from cysts about the pharynx of *Semotilus bullaris* Rafinesque. The

description (Stafford, 1904: 494) is not complete enough to permit one to decide whether it has to do with a species of Diplostomulum or Tetracotyle. No figure has been published.

2. *Diplostomum cobitidis* von Linstow

Tetracotyle cobitidis Mataré (1910: 497)

This species was described by von Linstow (1890: 179) from specimens found in thick-walled cysts in the body cavity of *Cobitis barbatula*. Here, again, no figure is given and the description is too brief to show whether the parasite is a Diplostomulum or a Tetracotyle. Zandt (1924: 239) reported the finding of *D. cobitidis* in *Cobitis barbatula* and *Cottus gobio* in the Bodensee and stated that, according to the key of Lühe, the parasite was probably a Tetracotyle. I have examined specimens from *Cottus gobio* which were designated by Dr. Zandt, of Konstanz, as *Diplostomum cobitidis* and presented to Professor La Rue. I find these worms to be tetracotyles, perhaps identical with *Tetracotyle ovata* von Linstow.

3. *Diplostomum* sp. Zandt

The description of this form is based on a single specimen found in the vitreous humor of *Coregonus fera* (Zandt, 1924, p. 240; Fig. 14) from the Bodensee, Konstanz. According to the figure, the worm has the form of *Diplostomulum spathaceum* with the body deeply constricted near the middle, anterior to the acetabulum. Otherwise in form and size it closely resembles *D. spathaceum*. It seems probable that the constriction is an artifact, due possibly to the presence of a girdle of connective tissue about the body. I have sometimes seen diplostomula, taken from the lenses of American fishes, with the body constricted in a similar manner, when they were in the act of passing through the lens capsule. So long as the lens and the capsule remain intact, a parasite can work its way through with ease if it once perforates the lens epithelium. If, however, a piece of the lens epithelium, containing a diplostomulum which has worked half through a pore in this epithelium, should be torn from the lens, the parasite

could no longer alter its position relative to that of the tissue about it. Lens epithelium is very delicate and a tiny strand of it embedded, as it were, in the infolded cuticula of the parasite would be hardly visible.

4. *Distomum coelebs* von Linstow

Agamodistomum coelebs Linstow — Stossich (1892: 176)

This worm was found encysted in the wall of the intestine of *Fringilla coelebs* and briefly described by von Linstow (1875: 192; Taf. III, fig. 15). Mataré (1910: 496) suggested that *Distomum coelebs* might be a larval strigeid. This supposition is supported by the fact that a large, bright, spherical structure, possibly a hold-fast organ, is located behind the acetabulum. The large size of the spines on the anterior part of the body and the brevity of the broad intestinal caeca are, however, characters not common to strigeid metacercariae. The finding of the species has been reported only once.

5. *Tetracotyle ardeae* Mataré

Geschlechtlich unentwickeltes Distoma — Wedl (1857: 247)
Distomum capsulare — Diesing (1858: 355)
Agamodistomum capsulare Diesing — Stossich (1892: 34)

This parasite was found encysted in the oesophagus, pectoral muscles, and under the skin of the head and neck of *Ardea purpurea, Ardea nycticorax, Ardea cinerea, Gallinula crex* and *Podiceps negricollis* and described by Wedl (1857: 247; Taf. I, fig. 8) as a sexually undeveloped distome. Mataré (1910: 496) regarded it as a strigeid metacercaria. According to the figure, the presence of a hind-body, a hold-fast organ, or calcareous corpuscles is not evident. The species is probably not a strigeid metacercaria. Pagenstecher (1857b: 246) found, but did not describe, a species of Tetracotyle encysted in the neck muscles of a wild duck.

6. *Monostomum constrictum* Diesing

Diplostomulum constrictum Dies. — Brandes (1892: 511)

This form was very briefly described by Diesing (1850: 322, and 1855: 62; Taf. II, figs. 3–5) from trematodes found

in the eyes of *Abramis brama*. According to the figures, the animal is apparently without an acetabulum and a hold-fast organ. The fact that the body is divided into distinct anterior and posterior regions by a constriction is hardly sufficient evidence to warrant the conclusion of Brandes (1892: 511) that the worm is a strigeid larva. Lühe (1909: 168) regarded it as a Tylodelphys. If *Monostomum constrictum* is a strigeid metacercaria at all, it probably belongs to the larval group Neascus, a conclusion suggested by the arrangement of the excretory vessels (Diesing, 1855; Taf. II, fig. 5).

7. *Distomum retroconstrictum* Srámek

The parasite described and figured by Srámek (1901: 108; Fig. 9) as *Distomum retroconstrictum* and regarded as identical with *Monostomum constrictum* Diesing is apparently a specimen of *Diplostomulum clavatum* with an accidental constriction near the anterior end. Srámek confused the anterior and posterior ends of the animal and misinterpreted the hold-fast organ for the mouth, and the mouth for the excretory pore.

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Explanation of Figures

ac —acetabulum
acv —anterior transverse commissural excretory vessel
al —anterior lateral excretory vessel
an —anterior nerve
apt —anterior primary collecting tubule
c —cuticula
cc —calcareous concretion
cmf —circular muscle fibers
ep —excretory pore
ed —excretory duct
gc —unicellular gland cell
hb —hind-body
hf —hold-fast organ
hfg —hold-fast gland
int —intestinal caecum
j —apparent point of union of primary excretory apparatus with reserve bladder
lc —lateral collecting vessel
lmf —longitudinal muscle fibers
ls —lateral sucker
md —median dorsal excretory vessel
oe —oesophagus
os —oral sucker
pc —posterior transverse commissural excretory vessel
ph —pharynx
pl —posterior lateral excretory vessel
pn —posterior nerve
ppt —posterior primary collecting tubule
rf —fundament of reproductive organs
sp —supra-pharyngeal nerve commissure
tb —tubular portion of urinary bladder
ub —urinary bladder

PLATE I

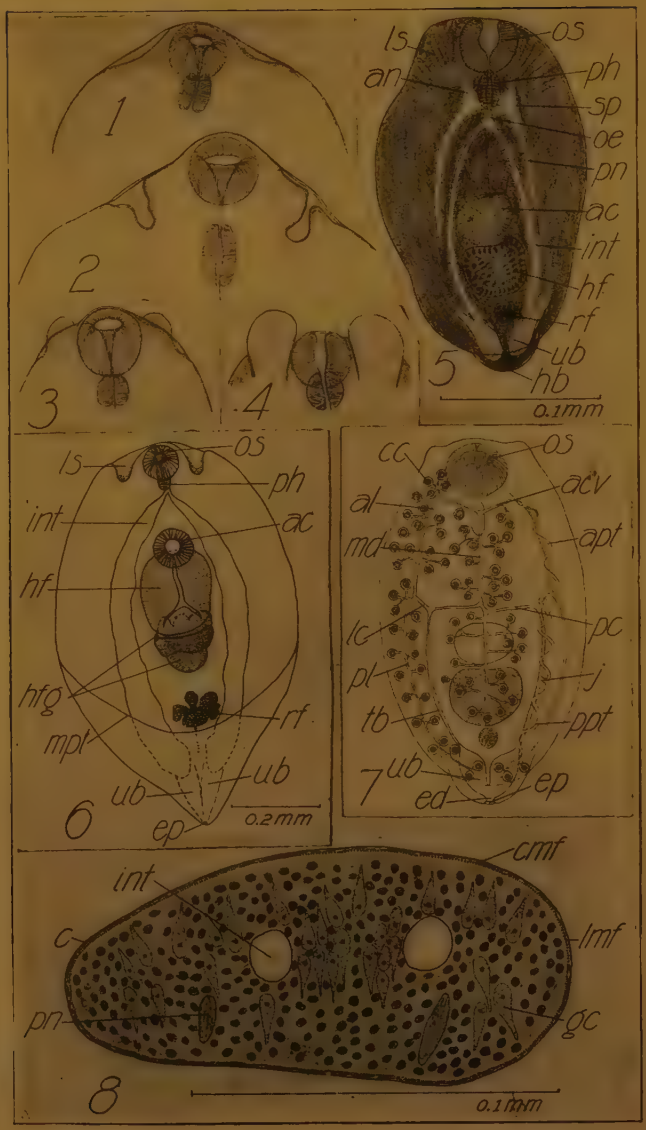
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PLATE I

Figures 1, 2, 3, 4 and 5 were drawn from specimens mounted *in toto* with the aid of a camera lucida and to the same magnification.

FIG. 1. *Diplostomulum spathaceum,* ventral view of the anterior end showing the lateral suckers as broad shallow depressions, the form in which they usually appear in preserved material

FIG. 2. *Diplostomulum petromyzi-fluviatilis,* ventral view of the anterior end showing the usual form of the lateral suckers in preserved specimens

FIG. 3. *Diplostomulum phoxini,* ventral view of the anterior end showing the usual form of the lateral suckers in preserved worms

FIG. 4. *Diplostomulum petromyzi-fluviatilis,* dorsal view of the anterior end of a specimen having the body much contracted laterally and the lateral suckers everted. This is an unusual condition in preserved specimens

FIG. 5. *Diplostomulum browni,* ventral view showing the salient morphological features and the lateral suckers as they usually appear in preserved specimens

FIG. 6. *Diplostomulum corti,* ventral view showing the principal internal structures. From a sketch made by Dr. W. W. Cort

FIG. 7. *Diplostomulum browni,* a semi-diagrammatic representation of the excretory system in dorsal view. Based upon a study of living specimens much flattened by cover-glass pressure

FIG. 8. *Diplostomulum browni,* cross-section through the fore-body just anterior to the acetabulum